

The use of demographic sensitivity analysis in marine species conservation planning

Leah R. Gerber ^{a,*}, Selina S. Heppell ^{b,1}

^a School of Life Sciences, Arizona State University, P.O. Box 871501, Tempe, AZ 85287-1501, USA

^b Department of Fisheries and Wildlife, Oregon State University, 104 Nash Hall, Corvallis, OR 97331, USA

Received 18 April 2003; received in revised form 17 November 2003; accepted 13 January 2004

Abstract

We explore the idea that a sensitivity analysis conducted on stage-specific demographic rates can be used to improve our ability to determine the efficacy of conservation plans that are designed to enhance the recovery of individual marine species. Because a given reserve may not be able to protect all life stages and habitats for wide-ranging marine organisms, reserves should target life history stages for which protection will foster the highest population growth rates. Likewise, it should be recognized that reserves designed to reduce mortality of a particular life stage, such as adults that are the focus of a fishery, will benefit some life history types more than others. For a representative range of marine life histories, we found that the change in λ resulting from a decrease in adult mortality varied for each species considered, with the largest positive impact on population growth in marine invertebrates and fish and lowest in species with very low adult mortality rates. Results from analyses of both mortality elasticity and absolute change in λ resulting from a decrease in adult mortality were highly correlated with adult survival rate and maximum fecundity, and also showed a significant relationship with age at sexual maturity, longevity and juvenile survival. Standardized demographic analysis may be a useful first step to compare disparate conservation goals for marine reserve design for species with distinct life histories.

© 2004 Elsevier Ltd. All rights reserved.

Keywords: Marine reserve; Demography; Sensitivity analysis; Life history

1. Introduction

Marine reserves are a relatively new approach to marine conservation, with the vast majority of literature on marine reserve theory published since 1992 (see Gerber et al., 2003 for review). To date, most models of marine reserves have focused on questions concerning fishery management, with most studies concluding that reserves increase yield when populations would otherwise be overfished. However, few of these existing single-species models have considered all life stages, thereby failing to acknowledge that most marine organisms are wide-ranging and have life history stages that occur in very different habitats. Much of the theory developed

for marine reserves has focused on issues of larval dispersal, very few studies have addressed the question, “for which types of species should reserves be most effective?”. Here we use standard stage structured population models (e.g., Caswell, 2001) to examine the potential efficacy of marine reserves that target particular life history stages or their habitats.

As yet, the designation of marine reserves for slow growing, long-lived species like marine mammals and seabirds has largely taken place without ecological input, and no-take zones for fishery recovery have not considered the conservation concerns of these species. At the same time, marine sanctuaries are being established worldwide based on their marine mammal or bird fauna (e.g., Southern Ocean Sanctuary, California sea otter game refuge). Charismatic organisms such as marine mammals or birds are often used as flagship species serving as guarantors of broad-scale conservation, and endangered species such as right whales or humpback whales are often used as flagships for National Marine

* Corresponding author. Tel.: +1-480-727-3109; fax: +1-480-965-2519.

E-mail addresses: leah.gerber@asu.edu (L.R. Gerber), selina.heppell@oregonstate.edu (S.S. Heppell).

¹ Tel.: +1-541-737-9039; fax: +1-541-737-3590.

Sanctuaries. However, there is little systematic theory for how to select, design and monitor these reserves. In protecting a specific population, the optimal protected area would encompass that population's year-round distribution. However, for the majority of marine species, the year round distribution of a population would cover a vast area. The question therefore becomes whether limited protection in specific parts of a species' range is worthwhile. Since several of the threats faced by marine mammals are either incremental (e.g., pollutant exposure) or instantaneous (e.g., acoustic pollution, fishery bycatch), the establishment of areas in which these species are protected for a portion of their lives will help to mitigate the effect of these threats. Indeed, there is empirical evidence that marine reserves may increase population vital rates for some fish and invertebrates (e.g., Duarte et al., 1996; Halpern, 2003). Field data are needed to determine whether reserves reduce mortality for long-lived vertebrates; we can then apply sensitivity analysis to determine whether the reduction in mortality translates to population level effects. In particular, demographic sensitivity analysis may be relevant to the question of when and how to protect different life-stages and distributional ranges to promote population protection.

Alternative designs for marine protected areas can be compared with demographic and ecological models before experimental reserves are established (Heppell and Crowder, 1998). Because life history information is lacking for many marine populations, categorizing life histories according to their response to changes in stage-specific mortality may provide a useful framework for considering conservation alternatives (Heppell et al., 2000; Jennings, 2000). One interesting facet of the reserve design debate is that most reserves are quite small in area, and represent only a small portion of the total range of species (Roberts et al., 2002). Thus, any decrease in stage-specific mortality for the target organism is likely to be quite low, making analytical perturbation analysis of life histories a relevant tool. As such mortality sensitivity analysis is an appropriate metric for analyzing the degree to which reserves that reduce take (through harvest or bycatch reduction) might actually increase the population growth rate (λ). In this paper, we show that insights from demographic sensitivity analysis can be used to predict a priori when marine reserves are likely to be most effective for a life history-type, and argue that perturbation analysis can serve as an early step in MPA planning. We examine the degree to which the effects of reducing adult mortality (the life-stage generally targeted in fisheries) via reserve establishment depends on a species' life history characteristics. Species were chosen as case studies representing a wide range of species with different life histories, and levels of mortality that could be reduced by protected areas. For example, closed areas have been used as a

conservation tool for the commercially important red sea urchin (Botsford et al., 1993; Pfister and Bradbury, 1996) and to protect important breeding habitats for the Federally-listed Steller sea lion (Bowen et al., 2001). We examine the degree to which such reductions in adult mortality depend on the life cycle in which this life stage is embedded.

2. Methods

To evaluate the degree to which reducing adult mortality depends upon the species life history in which this life stage is embedded, we constructed simple, age-structured transition matrices based on data or models from the literature for a wide range of marine species (Table 1). The models used an annual time step, with the exception of the intertidal snail, *Littorina*, whose life table was set in 3-month intervals (Hughes and Roberts, 1981). We then adopted two approaches to compare the effect of changes in adult mortality across species. First, we conducted perturbation analysis by using the analytical solution to the expected change in asymptotic population growth rate (λ) for small changes in mortality (the derivative $\partial\lambda/\partial\mu$, where μ is annual mortality). While this is a standard approach in demography, it is not generally recognized that this type of analysis yields different answers than the more commonly applied survival sensitivity analysis. Because the derivative gives most accurate changes in lambda for small changes in mortality, on the order of 1–10%, (de Kroon et al., 2000), this approach is intended to represent a reserve that reduces mortality for a small portion of the range of one life stage for a target species. Our second approach was a direct perturbation analysis of each matrix to calculate the change in λ for a much larger change in mortality, arbitrarily set at 20% as an example. Our intent was to examine differences in results when analytical or direct perturbation is applied, as recommended by Ehrlén and van Groenendael (1998). Finally, we ran regression analyses of the results of both perturbation analyses with common life history characteristics to search for patterns in the response of λ across life history types.

We use mortality sensitivity analysis instead of standard survival sensitivity analyses because this approach was more appropriate for analyzing the degree to which reserves reduce take (through harvest or bycatch reduction) and increase lambda (see also Fujiwara and Caswell, 2001; Kareiva et al., 2000). Simply stated, a proportional reduction in annual mortality (Q) is not equivalent to a proportional increase in annual survival (P), where $Q = (1 - P)$. For example, for an initial survival rate $P_{\text{init}} = 0.9$, a 10% increase yields a modified survival rate $P_{\text{new}} = 0.99$, whereas a 10% reduction in $Q = 0.1$ yields $P_{\text{new}} = 0.91$. For survival rates greater

Table 1

Life history parameters, estimated lambda values, general level of anthropogenic impact, and references for species considered in our analysis. ASM: age of first reproduction, ignoring precocial breeders. All parameters are annual rates, except for the intertidal snail, *Littorina*, whose model is based on a 3-month time step

Species	Maximum fecundity ^a	ASM	Longevity	Newborn survival ^b	Juvenile survival ^b	Adult survival	Lambda	Anthropogenic impacts	References
Orca	0.26	15	70	0.98	0.982	0.99	1.03	Moderate	Olesiuk et al. (1988)
Wandering Albatross	0.5	11	50	0.95	0.95	0.93	1.036	High	Croxall et al. (1990)
Gray whale	0.47	8	59	0.469	0.893	0.945	1.027	Moderate	Reilly (1984)
Leopard Shark	13.04	16	50	0.756	0.87	0.87	1.071	Moderate	Cailliet (1992)
Sei whale	0.27	5	60	0.933	0.934	0.942	1.009	Moderate	Smith (1977)
Loggerhead sea turtle	153	21	unknown	0.705	0.705	0.809	0.95	High	Crowder et al. (1994)
Kemp's ridley turtle	125	10	unknown	0.310	0.65	0.847	1.039	High	Heppell et al. (2003)
Harbor seal	0.92	5	35	0.40	0.87	0.894	0.995	Low	Reijnders (1978)
Northern sea lion	0.63	5	30	0.78	0.848	0.792	0.986	Moderate	York (1994)
<i>Littorina</i>	275	5	16	0.04	0.625	0.626	0.887	Low	Hughes and Roberts (1981)
Southern sea otter	0.9	3	20	0.46	0.75	0.89	0.984	Moderate	Eberhardt and Schneider (1994); Jameson and Johnson (1993); Riedman et al. (1994); Siniff and Ralls (1991)
Salmon ^c	5150	3	5	0.000287	0.057	0.729	0.76	High	Kareiva et al. (2000)
Red Sea Urchin ^d	2,000,000 ^e	3	50	n/a	0.5	0.72	1	Moderate	Pfister and Bradbury (1996)
Striped Bass	4,800,000	4	14	0.000007	0.6	0.6	1.002	High	Cohen et al. (1983)
North Sea Haddock ^f	400,000	3	6	0.000115	0.394	0.295	1.197	Moderate	Pitcher and Hart (1982)

^a Maximum fecundity rate (total offspring per year); for our pre-breeding census models fecundities were multiplied by 0.5 for offspring sex ratio and corresponding newborn survival rate.

^b Geometric mean survival rate of juvenile or adult age classes, defined by ASM.

^c Post-breeding census; semelparous; juvenile survival rate is for freshwater/estuary stage and first ocean stage (age 1–2); adult survival rate could technically include 0 for age 6.

^d Adults defined as stage 2 and 3 of 3 stage model; survival elasticity = sum of P and G elasticities for each stage; for 20% increase, P and G were raised according to $P = (1 - \text{gamma}) * \text{survival}$ and $G = \text{gamma} * \text{survival}$, where gamma is transition probability of survivors.

^e Fertility is age-specific to solve for lambda approximating 1.

^f Estimated from data between 1957 and 1967.

than 0.5, a change mortality will have a smaller effect on λ than the same proportional change in survival, and the opposite is true for survival rates less than 0.5. Formally, elasticity of survival is equal to the odds ratio for survival multiplied by the elasticity to mortality (Caswell, 2001)

$$E_P = \frac{P}{\lambda} \frac{\partial \lambda}{\partial P} = \left(\frac{-P}{1-P} \right) \frac{Q}{\lambda} \frac{\partial \lambda}{\partial Q}. \tag{1}$$

The elasticity of λ to changes in mortality (E_Q) can be calculated from the survival elasticity (E_P) as

$$E_Q = \frac{E_P}{P} (P - 1). \tag{2}$$

Adult survival elasticity ($E_{P_{ad}}$) can be calculated from a life cycle model using the eigenvectors of the transition matrix (Caswell, 2001). Alternatively, for simple age-structured models with constant survival and fertility for adult age classes, adult survival elasticity can be estimated as

$$E_{P_{ad}} = \frac{P_{ad}}{\alpha(\lambda - P_{ad}) + P_{ad}}, \tag{3}$$

where P_{ad} is mean adult annual survival and α is age at first reproduction (Heppell et al., 2000). This elasticity approximation eliminates the need for complete information on juvenile survival rates, which are often lacking for marine species. For our analyses, the relationship

between adult mortality elasticity and vital rates was obtained analytically using Eqs. (1)–(3). Specifically, we estimate survival elasticity with Eq. (3) and convert it to mortality elasticity with Eq. (2).

Second, because elasticity analysis focuses on small changes in adult mortality, we considered a second metric of reserve efficacy to determine whether relatively large changes in adult mortality (e.g., 20% reduction) would influence our interpretation of the relative impacts of a reserve across life history types. Here, we calculated the absolute difference in the dominant eigenvalue (λ) after reducing adult mortality by 20% (Ehrlén and van Groenendael, 1998). This approach, hereafter referred to as the simulation approach, included five steps: (1) record the baseline λ , (2) convert baseline survival rate into a mortality rate, (3) reduce adult mortality by 20%, (4) calculate modified λ , and (5) record the absolute difference between baseline and modified λ .

3. Results

The change in λ resulting from a decrease in adult mortality varied for each representative life history (Fig. 1). In general, marine invertebrates and fish exhibited the most striking response, while whales, alba-

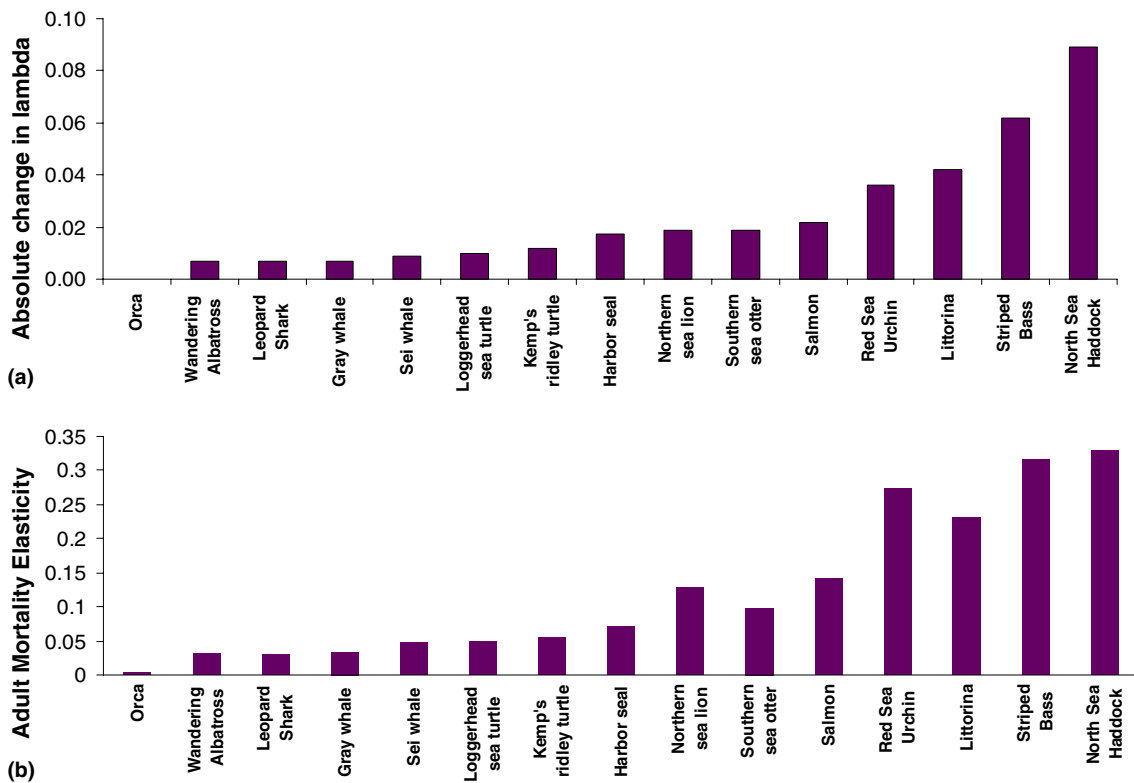


Fig. 1. Potential effects of marine reserves on 15 marine species, described as (a) absolute increase in λ with 20% decrease in adult mortality, and (b) adult mortality elasticity.

tross and sharks exhibited both low adult mortality elasticity and a very small absolute increase in λ following a decrease in adult mortality. Turtles, sea otters and pinnipeds were intermediate between these extremes. Results from the two analyses generally agree; however, there were some subtle differences for particular species. Fairly similar patterns were exhibited for those species that exhibited both small increases in lambda and low elasticity. Albatross, gray whales and leopard sharks had identical responses in the simulation; for the elasticity analysis leopard sharks had slightly higher elasticity than albatross and gray whales. Sea otters and sea lions exhibited a very similar response in the simulation, but otters had a much lower elasticity value as compared to sea lions in our second analysis.

We were interested in how both the predicted effect of a reduction in adult mortality from our two approaches might be explained by life history parameters, and secondly how life history parameters might explain inconsistent results between these approaches. First, we found that the two metrics of reserve efficacy were correlated for the 15 species examined in this analysis (Pearson's correlation coefficient $r = 0.937$, $p = 0.0001$). Simple linear regressions to examine the relationship between each response variable and various life history parameters showed a significant relationship between adult mortality elasticity and all life history attributes examined (Table 2). Of these attributes, mean adult survival and maximum fecundity showed the most significant effect, followed by age of sexual maturity and longevity, and juvenile survival. Slopes for all regressions were negative, except to fecundity, which was positive and very low. The significant but near zero value for this slope is a result of the wide range of values for fecundity (7 orders of magnitude) and a corresponding low range of values for the response variable. The highly significant relationship for adult survival and maximum fecundity for both response variables suggests that these life history attributes may be useful indicators of the potential efficacy of marine reserves.

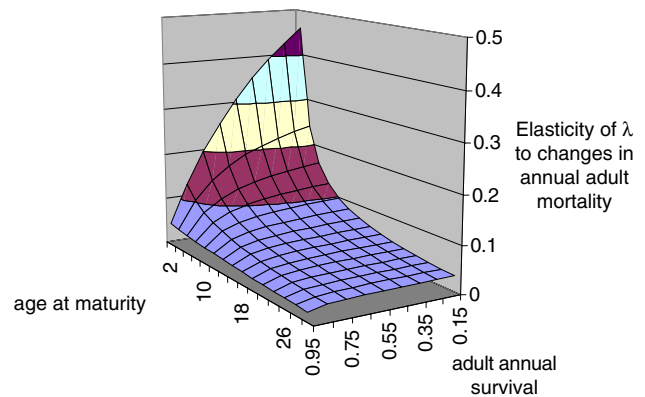


Fig. 2. Changes in adult mortality elasticity given by a simplified model with adults grouped into a single stage with mean fertility and annual survival (from Eqs. (2) and (3)).

The relationship between adult mortality elasticity and vital rates can be explained analytically using the elasticity approximation equation derived by Heppell et al. (2000, Fig. 2). Although this approximation technique does not account for age-specific survival and fertility rates that are common in marine species, Fig. 2 shows generally how mortality elasticity may be expected to change with age at maturity and adult annual survival rate. When adult survival is high, annual mortality is low and proportional changes in that rate have little impact, regardless of age at maturity. Intermediate and low adult survival rates result in a stronger response of λ to perturbations in mortality, and this effect increases with decreasing age at maturity. This relationship may shed light on the degree to which uncertainty in our estimates of α or P_{ad} will affect the interpretation of our results.

4. Discussion

Marine reserve planning for species of concern is difficult because (1) the demographic data on the species

Table 2

Results from regression analyses of life history attributes on (a) absolute increase in λ with 20% reduction in adult mortality and (b) adult mortality elasticity. Analysis done on absolute values of elasticities to facilitate comparison with results from simulation approach. Mean survival rates for juveniles and adults are geometric means from age-specific rates

	Absolute increase in λ with 20% reduction in adult mortality		Adult mortality elasticity	
	R^2	Slope	R^2	Slope
Mean juvenile survival	0.323	-0.055*	0.400	-0.280*
Mean adult survival	0.919	-0.129***	0.802	-0.552***
Ln(maximum fecundity)	0.619	0.003***	0.754	0.016***
Ln(ASM)	0.377	-0.022*	0.487	-0.116**
Ln(maximum age)	0.524	-0.021**	0.454	-0.089**

P values are symbolized as * for $p < 0.05$, ** for $p < 0.01$, and *** for $p < 0.001$. The two metrics of population response to changes in adult mortality were highly correlated for the 15 species examined in this analysis (Pearson's correlation coefficient $r = 0.937$, $p < 0.0001$).

is often limited, and (2) ontogenetic shifts and migrations are common for many species, so a single reserve is unlikely to reduce mortality for all life stages. Elasticity analysis of matrix models provides us with a useful tool for the early planning stages of reserve design. We can use the analytical form of the analysis, the derivative of population growth to a proportional change in mortality, in a comparative manner to determine which species are most likely to benefit from a reserve that reduces mortality in a particular life stage (e.g., adults). We can use a direct perturbation approach to assess the relative impact of larger proportional changes in mortality for particular species. The latter analysis may be particularly useful for determining the relative size of a reserve (and, hence, the proportion of the population that must be protected) to make a meaningful contribution to population growth and recovery. We can also use the matrix model approach to examine how life history characteristics (e.g., age at maturity, lifespan, fertility) correlate with the response of population growth rates to perturbations (Heppell et al., 2000; Saether and Bakke, 2000). This may be important for species with too little demographic information to construct even a simple life table.

In interpreting our results, we focus on identifying metrics that lead to measurable responses in order to categorize species life histories by their likely response. The two approaches we consider focus on reserves that seek to reduce adult mortality by small amounts (e.g., reserves covering only a small portion of a species range), and reserves that would result in large reductions in adult mortality (i.e., 20%). The few inconsistencies between panels A and B in Fig. 1 are consistent with results of Mills et al. (1999) and de Kroon et al. (2000), who suggest that significant changes in vital rates can yield different λ values than small changes, which are predicted from the derivative. We found little qualitative difference in the results from the two methods. Furthermore, both the mortality elasticity and perturbation approaches are well correlated for both adult survival rate and maximum fecundity (Table 2). Species with high fecundity exhibited the strongest response in our elasticity analysis (e.g., haddock), and species with a low adult survival rate exhibited the strongest recovery potential in the simulation. This suggests that for species threatened by anthropogenic factors, small reserves may benefit species with high fecundity but large reserves (e.g., that reduce mortality by 20%) are required for long-lived species with high adult survival. Both analyses suggest that adult and survival and maximum fecundity may be important life history parameters in determining reserve efficacy. Because age at sexual maturity, survival and longevity are correlated life history traits (Heppell et al., 2000), the relationship in our regressions was not surprising. Longevity probably shows a strong relationship for elasticity values because adult survival elasticity

is very high when the survival rate is close to λ , as it is for long-lived species (Heppell et al., 2000).

It is not surprising that long-lived, slow growing species with a high adult survival have low mortality elasticities and low potential for recovery. Furthermore, the demographic sensitivity analysis approach used in this study is not specific to marine reserves as a management tool (i.e., sensitivity analysis can be applied to examine a suite of hypothesized threats and potential management strategies). Yet, these “first principles” from demography and life history have rarely been considered in marine reserve design. This is very much a first step – to put our approach into practice, our results will need to be considered in the context of anthropogenic impacts and the relative impacts of alternative management plans. Nonetheless, in addition to metrics of population viability such as population size and variability in growth rate, demographic analyses can be used in designing monitoring frameworks for marine reserves focused on recovering overexploited populations. In particular, results from simple demographic analyses such as those described in this paper may help identify those species for which a given reduction in harvest of adults will substantially improve a population’s viability and those species that are unlikely to benefit from reserves.

Some of our results appear counter to those of previous studies that compare the elasticities of population growth to changes in survival rather than mortality (e.g., Heppell et al., 1999; Saether and Bakke, 2000). It is well established that fecundity elasticity will be high for shorter-lived species such as many fish and invertebrates and adult and juvenile survival elasticity will be high for long-lived species such as marine mammals, sea turtles and sea birds (Heppell et al., 2000, 1999; Russell, 1999; Saether and Bakke, 2000). Because survival rates are necessarily high for long-lived species, proportional changes in adult survival for marine mammals and sea birds generally have a large impact on population growth, and are expected to give a greater improvement in λ for these species than similar perturbations in short-lived species. This is not always the case when we examine the effect of a change in adult mortality, which is greatest in shorter-lived species (Table 2, Fig. 1). We argue that mortality reduction is the appropriate metric for questions about MPA design because harvest and bycatch reduction acts on individuals that die rather than on survivors. For example, Fujiwara and Caswell (2001) use mortality reduction to examine the impact of reducing mortality of right whales, and Kareiva et al. (2000) use a similar approach for salmon. Furthermore, reductions in mortality are more relevant for comparing species with a wide range of life histories because those with high annual survival rates, such as orca, cannot increase by more than a fraction of a percent without exceeding 1.0.

Elasticity analysis of deterministic matrix models as a management tool has supporters and critics (de Kroon et al., 2000; Mills et al., 2001; Ehrlen et al., 2001). Uncertainty in parameter estimates, annual variability in vital rates, and responses of vital rates to density are ignored in these analyses, although they could be incorporated in a more detailed modeling effort if data were available. Our intention is to encourage the formulation of a simple framework that compares potential responses across a wide range of species, which necessitates a simple modeling approach that provides qualitatively robust results. Uncertainty in vital rates is still critical to these results, however, and can be examined most easily with Fig. 2, which shows generally how the result (elasticity of λ to changes in adult mortality) is affected by changes in adult survival and age at maturity. While the breadth of life histories compared provides representation for our general conclusions regarding the efficacy of reserves for marine species, assessments for particular populations will require a more detailed analysis that considers uncertainty in model parameters, particularly adult mortality (longevity). Bootstrapping methods that produce a wide range of alternative models and distributions of elasticities could also be applied to this framework (see Caswell, 2001; Wisdom et al., 2000).

A useful first step in marine reserve design is to identify target species, and decide based on life history whether reserves are an appropriate conservation tool. If modeling results show that a 20% reduction in adult mortality fails to measurably increase λ , reserves that seek to reduce adult mortality may be the wrong approach. Elasticity analysis may be particularly useful as an initial management guide for marine reserve design because relatively few demographic data are required to put together a simple projection matrix (Caswell, 2001; de Kroon et al., 2000). In fact, estimates for survival elasticities can be generated without juvenile survival information if age at maturity and adult survival can be estimated (Heppell et al., 2000). However, as with applications of survival elasticity, our analysis should be applied with caution as a “first cut” for management recommendations, and primarily used for hypothesis generation and application to more complex models (de Kroon et al., 2000). Elasticity analysis of linear, deterministic projection matrices is generally robust to stochasticity but not to density dependence, where vital rates and λ are functions of population size. Future research should focus on analyses of mortality elasticities for different life histories and in variable environments. Moreover, the objectives sought for a particular reserve should focus on the life history attributes most likely to increase λ , and should reflect reasonable timeframes for realizing this effect. In summary, our analysis provides initial guidelines for comparing the potential effectiveness of

reserves that target particular life stages for a variety of species.

References

- Botsford, L. W., Quinn, J. F., Wing, S. R., Brittnacher, J. G. (1993). Rotating spatial harvest of a benthic invertebrate, the Red Sea Urchin, *Strongylocentrotus franciscanus*. Management of Exploited Fish—Alaska Sea Grant (pp. 409–428).
- Bowen, W. D., Harwood, J., Goodman, D., Swartzman, G. L. (2001). Review of the November 2000 biological opinion and incidental take statement with respect to the western stock of the steller seal lion, with comments on the draft August 2001 biological opinion. Final Report Prepared for North Pacific Fishery Management Council.
- Cailliet, G.M., 1992. Demography of the central California population of the leopard shark (*Triakis semifasciata*). *Australian Journal of Marine and Freshwater Research* 43, 183–193.
- Caswell, H., 2001. Matrix population models: construction, analysis, and interpretation. Sinauer Associates, Inc. 722 pp.
- Cohen, J.E., Christensen, S.W., Goodyear, C.P., 1983. A stochastic age-structured population model of striped bass (*Morone saxatilis*) in the Potomac river. *Canadian Journal of Fisheries and Aquatic Sciences* 40, 2170–2183.
- Crowder, L.B., Crouse, D.T., Heppell, S.S., Martin, T.H., 1994. Predicting the impact of turtle excluder devices on loggerhead sea turtle populations. *Ecological Applications* 4 (3), 437–445.
- Croxall, J.P., Rothery, P., Pickering, S.P.C., Prince, P.A., 1990. Reproductive performance, recruitment and survival of wandering albatrosses *Diomedea exulans* at Bird Island, South Georgia. *Journal of Animal Ecology* 59, 775–796.
- de Kroon, H., van Groenendael, J., Ehrlen, J., 2000. Elasticities: a review of methods and model limitations. *Ecology* 81, 607–618.
- Duarte, W.E., Ascencio, G., Moreno, C.A., 1996. Long-term changes in population density of *Fissurella picta* and *Fissurella limbata* (Gastropoda) in the marine reserve of Mehuin, Chile. *Revisita Chilena de Historia Natural* 69 (1), 45–56.
- Eberhardt, L.L., Schneider, K.B., 1994. Estimating sea otter reproductive rates. *Marine Mammal Science* 10 (1), 31–37.
- Ehrlén, J., van Groenendael, J., 1998. Direct perturbation analysis for better conservation. *Conservation Biology* 12, 470–474.
- Ehrlen, J., van Groenendael, J., de Kroon, H. 2001. Reliability of Elasticity Analysis: Reply to Mills et al. *Conservation Biology* 15 (1), 278–280.
- Fujiwara, M., Caswell, H., 2001. Demography of the endangered North Atlantic right whale. *Nature* 414 (6863), 537–541.
- Gerber, L.R., Botsford, L., Hastings, A., Possingham, H., Gaines, S., Palumbi, S., Andelman, S., 2003. Population models for reserve design: a retrospective and prospective synthesis. *Ecological Applications* 13, S47–64.
- Halpern, B.S., 2003. The impact of marine reserves: do reserves work and does reserve size matter? *Ecological Applications* 13, S117–S137.
- Heppell, S.S., Caswell, H., Crowder, L., 2000. Life histories and elasticity patterns: perturbation analysis for species with minimal demographic data. *Ecology* 81 (3), 654–665.
- Heppell, S. S., Crouse, D., Crowder, L., Epperly, S., Gabriel, W., Henwood, T., Marquez, R. (in press). A population model to estimate recovery time, population size and management impacts on Kemp's ridley sea turtles. *Chelonian Conservation and Biology*.
- Heppell, S.S., Crowder, L.B., 1998. Prognostic evaluation of enhancement programs using population models and life history analysis. *Bulletin of Marine Science* 62 (2), 495–507.

- Heppell, S.S., Crowder, L., Menzel, T.R., 1999. Life table analysis of long-lived marine species with implications for conservation and management. *American Fisheries Society Symposium* 23, 137–148.
- Hughes, R.N., Roberts, D.J., 1981. Comparative demography of *Littorina rudis*, *L. nigrolineata* and *L. neritoides* on three contrasted shores in North Wales. *Journal of Animal Ecology* 50, 251–268.
- Jameson, R.J., Johnson, A.C., 1993. Reproductive characteristics of female sea otters. *Marine Mammal Science* 9 (2), 156–167.
- Jennings, S., 2000. Patterns and prediction of population recovery in marine reserves. *Reviews in Fish Biology and Fisheries* 10 (2), 209–231.
- Kareiva, P., Marvier, M., McClure, M., 2000. Recovery and management options for spring/summer Chinook salmon in the Columbia River Basin. *Science* 290, 977–979.
- Mills, L.S., Doak, D.F., Wisdom, M.J., 1999. Reliability of conservation actions based on elasticity analysis of matrix models. *Conservation Biology* 13 (4), 815–829.
- Mills, L.S., Doak, D.F., Wisdom, M.J., 2001. Elasticity analysis for conservation decision making: Reply to Ehrlen et al. *Conservation Biology* 15 (1), 281–283.
- Olesiuk, P. F., Bigg, M. A., Ellis, G. M. (1988). Life history and population dynamics of resident killer whales (*Orcinus orca*) in the coastal waters of British Columbia and Washington state. *Rep. Int. Whal. Commn. Special Issue*. 12, pp. 209–243.
- Pfister, C.A., Bradbury, A., 1996. Harvesting red sea urchins: recent effects and future predictions. *Ecological Applications* 6(1), 298–310.
- Pitcher, T.J., Hart, P.J.B., 1982. *Fisheries ecology*. Chapman and Hall, London.
- Reijnders, P.J.H., 1978. Recruitment in the harbor seal *Phoca vitulina* population in the Dutch Wadden sea. *Netherlands Journal of Sea Research* 12, 164–179.
- Reilly, S. (1984). Observed and maximum rates of increase in gray whales, *Eschrichtius robustus*. *Rep. Int. Whal. Commn. Special Issue* 6, pp. 389–400.
- Riedman, M.L., Estes, J.A., Staedler, M.M., Giles, A.A., Carlson, D.R., 1994. Breeding patterns and reproductive success of California sea otters. *Journal of Wildlife Management* 58, 391–399.
- Roberts, C.M., McClean, C.J., Veron, J.E.N., Hawkins, J.P., Allen, G.R., McAllister, D.E., Mittermeier, C.G., Schueler, F.W., Spalding, M., Wells, F., Vynne, C., Werner, T.B., 2002. Marine biodiversity hotspots and conservation priorities for tropical reefs. *Science* 295, 1280–1284.
- Russell, R.W., 1999. Comparative demography of life history tactics of seabirds: implications for conservation and marine monitoring. *American Fisheries Society Symposium* 23, 51–76.
- Saether, B.E., Bakke, O., 2000. Avian life history variation and contribution of demographic traits to the population growth rate. *Ecology* 81 (3), 642–653.
- Siniff, D.B., Ralls, K., 1991. Reproduction, survival and tag loss in California sea otters. *Marine Mammal Science* 7, 211–229.
- Smith, T. (1977). Calculation of apparent increases in the Antarctic Sei whale population between 1930 and 1960. *Rep. Int. Whal. Commn. Special issue* 1, pp. 135–139.
- York, A.E., 1994. The population dynamics of northern sea lions, 1975–1985. *Marine Mammal Science* 10, 38–51.
- Wisdom, M.J., Mills, L.S., Doak, D.F., 2000. Life stage simulation analysis: estimating vital-rate effects on population growth for conservation. *Ecology* 81 (3), 628–641.